A multi-region nonlinear age–size structured fish population model

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Abstract

The goal of this paper is to present a generic multi-region nonlinear age-size structured fish population model, and to assess its mathematical well-posedness. An initial-boundary value problem is formulated. Existence and uniqueness of a positive weak solution is proved. Eventually, a comparison result is derived : the population of all regions decreases as the mortality rate increases in at least one region.

Key words: Population dynamics, age-size structure, system of partial differential equations, initial-boundary value problem, variational formulation, positivity.

1 Introduction

Fish population dynamics models are essential to provide assessment of the fish abundance and fishing pressure. Their use forms the basis of scientific advice for fisheries managements. Discrete age structured models are most of the time used for fisheries stock assessments [1]. Indeed, ecologists, mathematicians and population biologists have observed that the age structure provides more realistic results at reasonable computational expense for a wide variety of biological populations (see [2], [3], [4], [5]).
In this paper we study a model which was first designed to represent Atlantic bigeye tuna populations [6] but which is also generic enough to be potentially usefull for various fish species. Indeed, most fish populations share specific characteristics which have to be taken into account in order to model their dynamics in a realistic manner.
A first point concerning tuna fisheries is that they are highly heterogeneous

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in space and time. This has an important impact on their functioning. Important migrations of fish occur at various scales and fish movements have to be explicitly represented. Moreover, growth potentially varies with space that is to say with the region of the ocean under consideration. Hence, fishes of the same age can exhibit very different sizes depending of their various history. Consequently a spatialized approach taking explicitly into account the potential variability of growth in space has to be used.

A second point is that, because of non-uniform mortality over sizes, bias on both growth and mortality estimates may result from simply adding a gaussian size distribution to an age structured model as it is generally done. It is reasonable to think that the use of both age and size as structure variables should enable to overcome this difficulty.

These are some of the principal problems of current stock assessment models. That is why it is necessary to carry on the modelling effort by proposing and testing more complex models. This paper follows this direction and its purpose is twofold.

First we describe a synthetic and generic model of population dynamics in which both age and size are taken as structure variables and in which fish movements among spatial regions are explicitly represented. The model is a system of coupled partial differential equations. Nonlocal nonlinearities appear in the boundary conditions modelling recruitment that is to say the birth law or density dependent fish reproduction. The relative complexity of the model enables a direct and simultaneous comparison with all the data available for tuna fisheries such as catches, fishing efforts, size frequencies, tagging data, and otoliths increments. This paper does not aim at getting into all the details of the parameterizations used to represent a particular tuna population and we refer to [6] for these points.

Our second and most important goal is to assess the mathematical well-posedness of the model. The paper is organized as follows. The equations of the model are presented in Section 2. Sections 3, 4 and 5 deal with the mathematical analysis of the model. In Section 3 we formulate an initial-boundary value problem, introduce a variational formulation and state our main mathematical results. Existence of a unique weak solution is shown in Section 4. As often with nonlinear problems the proof uses a fixed point argument. The methodology follows the one proposed in [7] for a scalar equation. It has to be adapted in order to be able to deal with our nonlinear system. We also show positivity of the solution and give a comparison result in Section 5. Namely we prove that if the fish mortality rate increases in at least one geographic region then the population globally decreases in all regions.

2 The model

The dynamics of the population of fish is described through density functions $p_i(t,a,l)$ where time $t \in (0,T)$, age $a \in (0,A)$ and length $l \in (0,L)$ are continuous variables and the subscript $i \in [1:N]$ refers to the geographic zone or region under consideration. The number of fish of age between a_1 and a_2, of length between l_1 and l_2 at time t in region i is given by the integral

$$\int_{a_1}^{a_2}\int_{l_1}^{l_2} p_i(t,a,l)dlda,$$

Let us set $\mathcal{O} = (0,T) \times (0,A)$ and $\mathcal{Q} = \mathcal{O} \times (0,L)$. The time evolution of the population given by Eq. 1 includes the following processes.

In region i, as time goes on and fishes grow older, their length increases with a growth rate γ_i. In a fish population individuals of the same age can often differ markedly in size [8]. This variability in growth can result from many different mechanisms, including genetic or behavorial traits that confer different performances to individuals, and factors such as environmental heterogeneity and variability [9]. In fishery science, this variability is usually taken into account in age-structured models using a length-at-age relation perturbed by a Gaussian noise with a length dependent standard deviation (see for example [10]). The model discussed here is length-structured and uses a diffusion term in the length variable with dispersion rate d_i to account for individuals having the same age but different lengths. The advection-diffusion term in length can be seen as the limit of a random walk model in which each individual grows with an average velocity, but has at each time step a small binomial probability to grow faster or slower than this average (see the book by Okubo [11] for more details).

The model also describes mortality and migration of individuals. The mortality rate is split into natural mortality μ_i and fishing mortality f_i. Let also $m_{i\to j}$ be the migration rate of individuals going from region i to region j ($m_{i\to j} = 0$ if regions i and j are not adjacent).
The density functions p_i for $i \in [1:N]$ follow the balance law:

$$\begin{cases} \partial_t p_i(t,a,l) + \partial_a p_i(t,a,l) = \partial_l(d_i(t,a,l)\partial_l p_i(t,a,l)) - \partial_l(\gamma_i(t,a,l)p_i(t,a,l)) \\ \qquad + \sum_{j\neq i}^{N} m_{j\to i}(t,a,l)p_j(t,a,l) \\ \qquad -(\sum_{j\neq i}^{N} m_{i\to j}(t,a,l))p_i(t,a,l) \\ \qquad -(\mu_i(t,a,l) + f_i(t,a,l))p_i(t,a,l), \quad (t,a,l) \in \mathcal{Q}, \end{cases} \tag{1}$$

These equations have to be completed with initial and boundary conditions. Homogeneous Neumann boundary conditions at $l = 0$ and $l = L$ express the fact that the length of individuals can not reach negative values or values larger than L.

$$\partial_l p_i(t, a, 0) = \partial_l p_i(t, a, L) = 0, \quad (t, a) \in \mathcal{O}. \tag{2}$$

The initial age and size distribution is prescribed,

$$p_i(0, a, l) = p_i^0(a, l), \quad (a, l) \in (0, A) \times (0, L). \tag{3}$$

We also need a boundary condition for $a = 0$ that is to say a recruitment law. It is written as:

$$p_i(t, 0, l) = \beta_i(t, l, P_i(t)), \quad (t, l) \in (0, T) \times (0, L), \tag{4}$$

The length of recruited fish is assumed to lie between 0 and a small constant length L_b. Moreover we denote by L_m the minimal length of fishes which have reached maturity. L_b and L_m satisfy $0 < L_b < L_m < L$. The stock spawning biomass is calculated as

$$P_i(t) = \int_0^A \int_{L_m}^L w_i(t, a, l) p_i(t, a, l) dl da, \tag{5}$$

where w_i is a weighting function. Finally we use a Beverton and Holt [9] stock-recruitment relation in each region and obtain,

$$\beta_i(t, l, P) = \mathbb{1}_{[0,L_b]}(l) \psi_i(t) \frac{P}{\theta_i + P}, \tag{6}$$

where $\mathbb{1}_{[0,L_b]}$ is the usual characteristic function, $\theta_i > 0$ is a constant parameter and $\psi_i(t)$ is a given function of time used to parameterize fluctuations of the recruitment not taken into account in the Beverton and Holt relation.

3 Main assumptions and preliminary results

In this section we set the mathematical frame in which the analysis is conducted. We formulate the main assumptions which are made on the data of the model, give the definition of a weak solution to the initial-boundary value problem and state our results in Theorems 3.1 and 3.2.

3.1 Functional spaces

Let us introduce the functional spaces which we use in the remainder of this work.

The vectorial notation $\mathbf{p} = (p_1, ..., p_N)^T$ is used. The usual scalar product of two vectors $\mathbf{p}, \mathbf{q} \in \mathbb{R}^N$ is denoted by $\mathbf{p}.\mathbf{q}$ and the norm of $\mathbf{p}$ by $|\mathbf{p}|$.
$\mathbf{H}$ and $\mathbf{H}^1$ are the separable Hilbert spaces defined by $\mathbf{H} = (L^2(0, L))^N$ and $\mathbf{H}^1 = (H^1(0, L))^N$. $\mathbf{H}$ is equipped with the scalar product

$$(\mathbf{p}, \mathbf{q})_{\mathbf{H}} = \int_0^L \mathbf{p}(l).\mathbf{q}(l)dl.$$

We denote by $||.||_{\mathbf{H}}$ the induced norm on $\mathbf{H}$.
$\mathbf{H}^1$ is equipped with the scalar product

$$(\mathbf{p}, \mathbf{q})_{\mathbf{H}^1} = \int_0^L \mathbf{p}(l).\mathbf{q}(l)dl + \int_0^L \partial_l \mathbf{p}(l).\partial_l \mathbf{q}(l)dl.$$

We denote by $||.||_{\mathbf{H}^1}$, the induced norm on $\mathbf{H}^1$.
By $< ., . >$ we denote the duality between $\mathbf{H}^1$ and its dual $(\mathbf{H}^1)'$.
$L^2(\mathcal{O}, \mathbf{H})$ (resp. $L^2(\mathcal{O}, \mathbf{H}^1)$) denotes the Hilbert space of measurable functions of $\mathcal{O}$ with values in $\mathbf{H}$ (resp. $\mathbf{H}^1$) such that
$||\mathbf{p}||_{L^2(\mathcal{O},\mathbf{H})} = (\int_{\mathcal{O}} ||\mathbf{p}(t, a, .)||^2_{\mathbf{H}} dtda)^{1/2} < \infty$ (resp. $||\mathbf{p}||_{L^2(\mathcal{O},\mathbf{H}^1)} < \infty$).
We also make use of the notation $V = L^2(\mathcal{O}, \mathbf{H}^1)$ and the dual space $V' = L^2(\mathcal{O}, (\mathbf{H}^1)')$. By $<< ., . >>$ we denote the duality between V and its dual V'.
The partial derivatives ∂_t and ∂_a denote differentiation in $\mathcal{D}'(\mathcal{O}, (\mathbf{H}^1)')$ and D stands for $\partial_t + \partial_a$.
We will have to use he following trace result.

Lemma 3.1 *Let $\mathbf{p}, \mathbf{q} \in V$ such that $D\mathbf{p}, D\mathbf{q} \in V'$. It holds that:*
For all $t_0 \in (0, T)$ and all $a_0 \in (0, A)$, $\mathbf{p}$ has a trace at $t = t_0$ belonging to $(L^2((0, A) \times (0, L)))^N$ and at $a = a_0$ belonging to $(L^2((0, T) \times (0, L)))^N$. The trace applications are continuous in the strong and weak topology. Moreover the following integration by parts formula holds,

$$\begin{aligned}\int_{\mathcal{O}} [< D\mathbf{p}, \mathbf{q} > + < D\mathbf{q}, \mathbf{p} >] dtda = & \int_0^A \int_0^L [\mathbf{p}.\mathbf{q}(T, a, l) - \mathbf{p}.\mathbf{q}(0, a, l)] dadl \\ & + \int_0^T \int_0^L [\mathbf{p}.\mathbf{q}(t, A, l) - \mathbf{p}.\mathbf{q}(t, 0, l)] dtdl\end{aligned}$$

Proof: This result is the extension to dimension N of Lemma 0 in [12]. Also see [13]. $\square$

We will also have to consider the space $\mathbf{L}^\infty = (L^\infty(\mathcal{Q}))^N$. $L^\infty(\mathcal{Q})$ is a Banach space equipped with the norm $||p_i||_\infty = \inf\{M; |p_i(t, a, l)| \leq M \text{ a.e. in } \mathcal{Q}\}$. Similarly $\mathbf{L}^\infty$ is a Banach space equipped with the norm $||\mathbf{p}||_\infty = \underset{i \in [1:N]}{max} ||p_i||_\infty$.

The movements rates $m_{i\to j}$ are assumed to satisfy

- $m_{i\to j}(t,a,l) \geq 0$ a.e in $\mathcal{Q}$, $m_{i\to j} \in L^\infty(\mathcal{Q})$.

We define the matrix of movements $\mathbf{M}$ by

$$M_{ij} = \begin{cases} m_{j\to i} & \text{if } i \neq j, \\ -\sum_{k\neq i}^{N} m_{i\to k} & \text{if } i = j. \end{cases}$$

Hence the term, $[\sum_{j\neq i}^{N} m_{j\to i}p_j - (\sum_{j\neq i}^{N} m_{i\to j})p_i]$, in Eq. 1 can be written in matrix form as $(\mathbf{Mp})_i$.
Concerning the diffusion coefficients d_i, the growth rates γ_i and the natural and fishing mortality rates μ_i and f_i, we make the following assumptions for all $i \in [1:N]$:

- $d_i(t,a,l) \geq d^0 > 0$, a.e in $\mathcal{Q}$, $d_i \in L^\infty(\mathcal{Q})$,
- $\gamma_i(t,a,l)$ is differentiable with respect to l, and $\gamma_i, \partial_l\gamma_i \in L^\infty(\mathcal{Q})$,
- $\mu_i(t,a,l), f_i(t,a,l) \geq 0$, a.e in $\mathcal{Q}$, $\mu_i, f_i \in L^\infty(\mathcal{Q})$. We also make use of the notation $z_i = \mu_i + f_i$.

In the formulation of the recruitment process (Eq. 4) ψ_i and w_i satisfy:

- $\psi_i(t) \geq 0$ a.e in $(0,T)$ and $\psi_i \in L^\infty(0,T)$,
- $w_i(t,a,l) \geq 0$ a.e in $\mathcal{Q}$ and $w_i \in L^\infty(\mathcal{Q})$.

The initial distributions $p_i^0(a,l)$ satisfies for all $i \in [1:N]$:

- $p_i^0(a,l) \geq 0$ a.e in $\mathcal{Q}$, $p_i^0 \in L^2((0,A)\times(0,L))$.

In order to prove our existence result it is convenient to perform a change of unknown function: $\mathbf{p}$ satisfies (1)-(4) if and only if $\hat{\mathbf{p}} = e^{-\lambda t}\mathbf{p}$ is a solution to the same system where $-(\mu_i + f_i)p_i$ is replaced $-(\mu_i + f_i + \lambda)p_i$ in Eq. 1 and β_i in the expression of the boundary condition at $a = 0$ (Eq. 4) is replaced by

$$\hat{\beta}_i(t,l,\hat{P}_i(t)) = \mathbb{1}_{[0,L_b]}(l)\psi_i(t)\frac{\hat{P}_i(t)}{\theta_i e^{-\lambda t} + \hat{P}_i(t)}, \tag{7}$$

$$\hat{P}_i(t) = \int_0^A \int_{L_m}^L w_i(t,a,l)\hat{p}_i(t,a,l)dlda. \tag{8}$$

In the remaining part of this paper this change of unknown is implicitly done and we omit the $\hat{p}_i$ notation. The constant λ will be fixed to a convenient value below. Moreover, the possible nullification of the term $\theta_i e^{-\lambda t} + \hat{P}_i(t)$, invites us to define,

$$\beta_i(t, l, P_i(t)) = \mathbb{1}_{[0,L_b]}(l)\psi_i(t)\frac{P_i(t)}{\theta_i e^{-\lambda t} + |P_i(t)|}. \tag{9}$$

This formulation will be used in the following. We will show that if initial distributions, p_i^0 are nonnegative then $p_i \geq 0$ a.e. in $\mathcal{Q}$, thus the two formulations are equivalent.

3.3 Variational formulation and weak solutions

Formally multiplying Eq. 1 by a function q_i and integrating by parts on $(0, L)$ yields to the definition of the following linear forms. For $p_i, q_i \in H^1(0, L)$ let us define,

$$b_i(p_i, q_i) = \int_0^L d_i \partial_l p_i \partial_l q_i dl + \int_0^L \gamma_i(\partial_l p_i) q_i dl + \int_0^L (z_i + \partial_l \gamma_i + \lambda) p_i q_i dl, \tag{10}$$

$$c_i(\mathbf{p}, q_i) = -\int_0^L (\mathbf{M}\mathbf{p})_i q_i dl, \tag{11}$$

$$e_i(\mathbf{p}, q_i) = b_i(p_i, q_i) + c_i(\mathbf{p}, q_i) \tag{12}$$

Summing over i, we define for $\mathbf{p}, \mathbf{q} \in \mathbf{H}^1$, the bilinear form $e(\mathbf{p}, \mathbf{q})$ by,

$$e(\mathbf{p}, \mathbf{q}) = \sum_{i=1}^N e_i(\mathbf{p}, q_i) \tag{13}$$

Lemma 3.2 *For* $\lambda > (\frac{1}{2d^0}||\gamma||_\infty^2 + ||\partial_l \gamma||_\infty^2 + N||\mathbf{M}||_\infty)$*, the bilinear form* $e(.,.)$ *is continuous and coercive on* $\mathbf{H}^1 \times \mathbf{H}^1$*, i.e there exist constants* $C_1 > 0$ *and* $C_2 > 0$ *such that*

$$|e(\mathbf{p}, \mathbf{q})| \leq C_1 ||\mathbf{p}||_{\mathbf{H}^1} ||\mathbf{q}||_{\mathbf{H}^1}, \ \forall \mathbf{p}, \mathbf{q} \in \mathbf{H}^1, \tag{14}$$

$$e(\mathbf{p}, \mathbf{p}) \geq C_2 ||\mathbf{p}||_{\mathbf{H}^1}^2, \ \forall \mathbf{p} \in \mathbf{H}^1. \tag{15}$$

Proof: Using Cauchy-Schwarz inequality we obtain,

$$|\sum_i b_i(p_i, q_i)| \leq (||\mathbf{d}||_\infty + ||\boldsymbol{\gamma}||_\infty + ||\mathbf{z}||_\infty + ||\partial_l \boldsymbol{\gamma}||_\infty + \lambda)||\mathbf{p}||_{\mathbf{H}^1}||\mathbf{q}||_{\mathbf{H}^1}$$

and

$$|\sum_i c_i(\mathbf{p}, q_i)| = |\sum_i \sum_j \int_0^L M_{ij} p_j q_i dl| \leq ||\mathbf{M}||_\infty N ||\mathbf{p}||_{\mathbf{H}^1} ||\mathbf{q}||_{\mathbf{H}^1}.$$

which proves (14).
Again using Cauchy-Schwarz inequality yields

$$|\int_0^L \gamma_i \partial_l p_i p_i| dl \leq ||\gamma||_\infty ||\partial_l p_i||_{L^2(0,L)} ||p_i||_{L^2(0,L)}.$$

Young's inequality then gives for any $\alpha > 0$

$$|\int_0^L \gamma_i \partial_l p_i p_i dl| \leq \frac{\alpha}{2} ||\partial_l p_i||^2_{L^2(0,L)} + \frac{1}{2\alpha} ||\gamma||^2_\infty ||p_i||^2_{L^2(0,L)}.$$

Therefore we have that

$$\sum_i \int_0^L \gamma_i \partial_l p_i p_i dl \geq -\frac{\alpha}{2} ||\partial_l \mathbf{p}||^2_{\mathbf{H}} - \frac{1}{2\alpha} ||\gamma||^2_\infty ||\mathbf{p}||^2_{\mathbf{H}}.$$

Now since μ_i and f_i are positive and d_i is bounded below by d^0, it follows that

$$e(\mathbf{p}, \mathbf{p}) \geq (d^0 - \frac{\alpha}{2}) ||\partial_l \mathbf{p}||^2_{\mathbf{H}} + (\lambda - (\frac{1}{2\alpha} ||\gamma||^2_\infty + ||\partial_l \gamma||^2_\infty + N||\mathbf{M}||_\infty)) ||\mathbf{p}||^2_{\mathbf{H}}.$$

It is possible to choose $\alpha = d^0$ and λ such that $\lambda^0 = (\lambda - (\frac{1}{2d^0} ||\gamma||^2_\infty + ||\partial_l \gamma||^2_\infty + N||\mathbf{M}||_\infty)) > 0$ and $C_2 = min(\frac{d^0}{2}, \lambda^0)$. □

We can now give the definition of a weak solution to the initial-boundary value problem (1)-(4) and state the results which are shown in Section 4 and 5. A weak solution to the initial-boundary value problem (1)-(4) is a vector valued function $\mathbf{p}$ satisfying the following **problem (P)**:
Find

$$\mathbf{p} \in V, \text{ such that } D\mathbf{p} \in V', \tag{16}$$

solution of

$$\int_{\mathcal{O}} < D\mathbf{p}, \mathbf{q} > dtda + \int_{\mathcal{O}} e(\mathbf{p}, \mathbf{q}) dtda = 0, \ \forall \mathbf{q} \in V, \tag{17}$$

$$\mathbf{p}(0, a, l) = \mathbf{p}^0(a, l) \quad \text{a.e in } (0, A) \times (0, L), \tag{18}$$

$$\mathbf{p}(t, 0, l) = \beta(t, l, \mathbf{P}(t)) \quad \text{a.e in } (0, T) \times (0, L). \tag{19}$$

In Section 4 it is proved that:

Theorem 3.1 *There exists a unique solution* $\mathbf{p}$ *to* **problem (P)**.

Notation: $\mathbf{p}(t, a, l)$ and $\mathbf{q}(t, a, l)$ being vector valued functions, $\mathbf{p} \leq \mathbf{q}$ means that $p_i \leq q_i$ a.e. in $\mathcal{Q}$ for all $i \in [1 : N]$.
With this notation, it is proved in Section 5 that:

Theorem 3.2 *The solution,* $\mathbf{p}$*, to* **problem (P)** *is nonnegative a.e in* $\mathcal{Q}$*. Moreover, let* $\mathbf{p}^1$ *(resp.* $\mathbf{p}^2$*) denote the solution to* **problem (P)** *associated with the vector of mortality rates* $\mathbf{z}^1$ *(resp.* $\mathbf{z}^2$*). If* $\mathbf{z}^1 \leq \mathbf{z}^2$ *then* $\mathbf{p}^2 \leq \mathbf{p}^1$*.*

4 Existence and uniqueness

The proof of existence and uniqueness consists in two main steps. First we show the result in the case of a constant recruitment (independent of the fish density). Second a fixed point argument enables to cope with the original nonlinear recruitment.

Lemma 4.1 *Let* $\mathbf{b}$ *be fixed in* $L^2((0,T)\times(0,L))^N$*. There exists a unique* $\mathbf{p}$ *satisfying (16)-(18) of* **problem (P)** *in which the initial condition (19) is replaced by* $\mathbf{p}(t,0,l) = \mathbf{b}(t,l)$ a.e in $(0,T)\times(0,L)$.

Proof: The proof is an adaptation of the results given for the scalar case in [7]. We sketch it for the sake of completeness. It consists in two steps.

Step 1: We prove that given $\mathbf{h} \in V'$ there exists a unique $\mathbf{p} \in V$, $D\mathbf{p} \in V'$ such that

$$\int_{\mathcal{O}} < D\mathbf{p}, \mathbf{q} > dtda + \int_{\mathcal{O}} e(\mathbf{p},\mathbf{q}) dtda = \int_{\mathcal{O}} < \mathbf{h}, \mathbf{q} > dtda, \quad \forall \mathbf{q} \in V \qquad (20)$$

and $\mathbf{p}(0,a,l) = \mathbf{p}(t,0,l) = 0$.

Let A^0 be the unbounded linear operator on $(L^2(\mathcal{Q}))^N$ with domain $D(A^0) = \{\mathbf{p} \in (L^2(\mathcal{Q}))^N,\ \partial_t\mathbf{p} + \partial_a\mathbf{p} \in (L^2(\mathcal{Q}))^N, \mathbf{p}(0,t,l) = \mathbf{p}(t,0,l) = 0\}$, defined by $\mathbf{p} \in D(A^0),\ A^0\mathbf{p} = \partial_t\mathbf{p} + \partial_a\mathbf{p}$. Then $-A^0$ is the infinitesimal generator of a contraction semigroup, $(S(\tau)\mathbf{p},\ \tau \geq 0)$, in $(L^2(\mathcal{Q}))^N$ (see [14]) and

$$(S(\tau)\mathbf{p})(t,a,l) = \begin{cases} \mathbf{p}(t-\tau, a-\tau, l) & \text{if } (t-\tau, a-\tau, l) \in \mathcal{Q}, \\ 0 \quad \text{otherwise.} \end{cases}$$

From this one can deduce that the unbounded linear operator A from V to V' with domain $D(A) = \{\mathbf{p} \in V,\ D\mathbf{p} \in V',\ \mathbf{p}(0,a,l) = \mathbf{p}(t,0,l) = 0\}$, defined by $A\mathbf{p} = D\mathbf{p}$ is a maximal monotone operator.
With the bilinear form $e(.,.)$ we can define a linear bounded and coercive operator E from V to V' such that $<< E\mathbf{p}, \mathbf{q} >>= \int_{\mathcal{O}} e(\mathbf{p},\mathbf{q}) dtda, \quad \forall \mathbf{p}, \mathbf{q} \in V$. Since E is bounded and coercive and A is maximal monotone we conclude that for any $\mathbf{h} \in V'$ there exists a unique $\mathbf{p} \in D(A)$ solution to $A\mathbf{p} + E\mathbf{p} = \mathbf{h}$

which is an abstract formulation of our problem because
$<< A\mathbf{p}, \mathbf{q} >>= \int_{\mathcal{O}} < D\mathbf{p}, \mathbf{q} > dtda, \quad \forall \mathbf{p} \in D(A), \ \forall \mathbf{q} \in V.$

Step 2: Let us now introduce a sequence of functions $\boldsymbol{\phi}^n \in (C^\infty(\overline{\mathcal{Q}}))^N$ such that

$$\boldsymbol{\phi}^n(0,a,l) \to \mathbf{p}^0(a,l) \quad \text{in } (L^2((0,A)\times(0,L)))^N,$$
$$\boldsymbol{\phi}^n(t,0,l) \to \mathbf{b}(t,l) \quad \text{in } (L^2((0,T)\times(0,L)))^N,$$

From **step 1**, we conclude that there exists a unique $\mathbf{q}^n$ in $D(A)$ solution to $A\mathbf{q}^n + E\mathbf{q}^n = -A\boldsymbol{\phi}^n - E\boldsymbol{\phi}^n$. Therefore $\mathbf{p}^n = \mathbf{q}^n + \boldsymbol{\phi}^n$ is a solution to (17) satisfying $\mathbf{p}^n(0,a,l) = \boldsymbol{\phi}^n(0,a,l)$ and $\mathbf{p}^n(t,0,l) = \boldsymbol{\phi}^n(t,0,l)$.
Now taking $\mathbf{p}^n$ as a test function in (17), integrating by parts using Lemma 3.1 and using the coercivity of $e(.,.)$ we obtain that

$$C_2||\mathbf{p}^n||_V^2 \leq \frac{1}{2}||\boldsymbol{\phi}^n(0,a,l)||^2_{(L^2((0,A)\times(0,L)))^N} + \frac{1}{2}||\boldsymbol{\phi}^n(t,0,l)||^2_{(L^2((0,T)\times(0,L)))^N}.$$

By the choice of $\boldsymbol{\phi}^n$ this implies that $\mathbf{p}^n$ is a bounded sequence in V. Therefore we can extract a subsequence still denoted $\mathbf{p}^n$ such that $\mathbf{p}^n \to \mathbf{p}$ weakly in V and $D\mathbf{p}^n \to \mathbf{r}$ weakly in V'. Since the operator D is continuous on $\mathcal{D}'(\mathcal{O}, (\mathbf{H}^1)')$, $\mathbf{r} = D\mathbf{p}$. Moreover since E is continuous $E\mathbf{p}^n \to E\mathbf{p}$. We conclude that $\mathbf{p}$ satisfies (17). The continuity of the trace applications on $t = 0$ and $a = 0$ implies that $\mathbf{p}(0,a,l) = \mathbf{p}^0(a,l)$ and $\mathbf{p}(t,0,l) = \mathbf{b}(t,l)$. $\square$

Lemma 4.2 *Let* $C_3 = (\max_{i\in[1:N]}[AL^2||\boldsymbol{\psi}||^2_\infty||\mathbf{w}||^2_\infty(\frac{e^{\lambda T}}{\theta_i})^2])^{1/2}$, *then the application*
$(p_i(t,a,l)) \mapsto (\beta_i(t,l,P_i(t)))$ *(cf Eqs 8 and 9) defines a bounded nonlinear operator, lipschitz continuous from* $L^2(\mathcal{O},\mathbf{H})$ *to* $(L^2((0,T)\times(0,L))^N$ *with lipschitz constant* C_3*.*

Proof: The application, $p_i(t,a,l) \mapsto P_i(t) = \int_0^A \int_{L_m}^L w_i(t,a,l)p_i(t,a,l)dadl$, defines a bounded linear operator from $L^2(\mathcal{Q})$ to $L^2(0,T)$. This follows from,

$$|\int_0^A \int_{L_m}^L w_i(t,a,l)p_i(t,a,l)dadl| \leq \int_0^A \int_0^L |w_i(t,a,l)p_i(t,a,l)|dadl,$$

and using Cauchy-Schwarz yields

$$\int_0^T |P_i(t)|^2 dt \leq ||\mathbf{w}||^2_\infty AL||p_i||^2_{L^2(\mathcal{Q})}.$$

The application $p_i(t,a,l) \mapsto \beta_i(t,l,P_i(t))$ defines a bounded nonlinear operator from $L^2(\mathcal{Q})$ to $L^2((0,T)\times(0,L))$. This follows from the fact that the application $u_i(t,P)=\dfrac{P}{\theta_i e^{-\lambda t}+|P|}$ from $[0,T]\times\mathbb{R}$ to $\mathbb{R}$ satisfies $|u_i(t,P)|\leq \dfrac{e^{\lambda T}}{\theta_i}|P|$ and therefore we have

$$\int_0^T\int_0^L(\beta_i(t,l,P_i(t)))^2dtdl \leq ||\boldsymbol{\psi}||_\infty^2(\frac{e^{\lambda T}}{\theta_i})^2||\mathbf{w}||_\infty^2 AL^2||p_i||^2_{L^2(\mathcal{Q})}.$$

Lipschitz continuity follows from the fact that $(t,P)\mapsto u_i(t,P)$ is lipschitz continuous in P uniformly in $t\in[0,T]$,

$$|u_i(t,P^1)-u_i(t,P^2)|\leq \frac{e^{\lambda T}}{\theta_i}|P^1-P^2|,\quad \forall P^1,P^2\in\mathbb{R},\ \forall t\in[0,T].$$

Hence, if to p_i^1 (resp. p_i^2) we associate P_i^1 (resp. P_i^2) it holds that

$$\begin{aligned}
&\int_0^T\int_0^L[\beta_i(t,l,P_i^1(t))-\beta_i(t,l,P_i^2(t))]^2dtdl\\
&=\int_0^T\int_0^L[\mathbb{1}_{[0,L_b]}(l)\psi_i(t)(u_i(t,P_i^1(t))-u_i(t,P_i^2(t)))]^2dtdl,\\
&\leq L||\boldsymbol{\psi}||_\infty^2(\frac{e^{\lambda T}}{\theta_i})^2\int_0^T|P_i^1(t)-P_i^2(t)|^2dt,\\
&\leq AL^2||\boldsymbol{\psi}||_\infty^2||\mathbf{w}||_\infty^2(\frac{e^{\lambda T}}{\theta_i})^2||p_i^1-p_i^2||^2_{L^2(\mathcal{Q})}.
\end{aligned}$$

□

Lemma 4.3 *There exists a unique* $\mathbf{p}$ *satisfying* **problem (P)**

Proof: Let $\hat{\mathbf{p}}$ be given in V. With $\hat{\mathbf{p}}$ we associate a vector $(\hat{P}_i(t))$. Let us denote $\mathcal{F}\hat{\mathbf{p}}=\mathbf{p}$ the solution to (16)-(18) and satisfying $(p_i(t,0,l))=(\beta_i(t,l,\hat{P}_i(t))$. From Lemma 4.1 and Lemma 4.2 we deduce that the nonlinear operator $\mathcal{F}$ maps V into itself. Moreover it follows from Lemma 3.1 that

$$\int_{\mathcal{O}}<D\mathbf{p},\mathbf{p}>dtda\geq -\frac{1}{2}\int_0^A||\mathbf{p}^0(a,.)||^2_{\mathbf{H}}da-\frac{1}{2}\int_0^T||\mathbf{p}(t,0,.)||^2_{\mathbf{H}}dt$$

The coercivity of $e(.,.)$ leads to

$$C_2\int_{\mathcal{O}}||\mathbf{p}(t,a,.)||^2_{\mathbf{H}^1}dtda\leq\frac{1}{2}\int_0^A||\mathbf{p}^0(a,.)||^2_{\mathbf{H}}da+\frac{1}{2}\int_0^T||\mathbf{p}(t,0,.)||^2_{\mathbf{H}}dt.$$

Lemma 4.2 then gives

$$C_2\int_{\mathcal{O}}||\mathbf{p}(t,a,.)||^2_{\mathbf{H}^1}dtda\leq\frac{1}{2}\int_0^A||\mathbf{p}^0(a,.)||^2_{\mathbf{H}}da+\frac{1}{2}C_3||\hat{\mathbf{p}}||^2_{L^2(\mathcal{O},\mathbf{H})},$$

and $\mathcal{F}$ is bounded from $L^2(\mathcal{O},\mathbf{H})$ to V.
The solutions we are looking for are the fixed points of $\mathcal{F}$. Let us show that

$\mathcal{F}$ is a strict contraction in $L^2(\mathcal{O}, \mathbf{H})$.
Let $\hat{\mathbf{p}}^1$ and $\hat{\mathbf{p}}^2$ be given in $L^2(\mathcal{O}, \mathbf{H})$ and let $\mathbf{p}^1 = \mathcal{F}\hat{\mathbf{p}}^1$ and $\mathbf{p}^2 = \mathcal{F}\hat{\mathbf{p}}^2$ be the associated solutions. The difference $\mathbf{p} = \mathcal{F}\hat{\mathbf{p}}^1 - \mathcal{F}\hat{\mathbf{p}}^2$ satisfies (16),(17), $\mathbf{p}(0, a, l) = 0$ and $(p_i(t, 0, l)) = (\beta_i(t, l, \hat{P}_i^1(t)) - \beta_i(t, l, \hat{P}_i^2(t)))$.
At the end of the proof of Lemma 3.2, since λ is arbitrary, one can choose $\lambda = \lambda_1 + \lambda_2$ with $\lambda_1 > \dfrac{1}{2d^0}||\gamma||_\infty^2 + ||\partial_l\gamma||_\infty^2 + N||\mathbf{M}||_\infty$ and $\lambda_2 > 0$ arbitrary. Hence,

$$e(\mathbf{p}, \mathbf{p}) \geq \tilde{C}_2||\mathbf{p}||_{\mathbf{H}^1}^2 + \lambda_2||\mathbf{p}||_{\mathbf{H}}^2 \geq \lambda_2||\mathbf{p}||_{\mathbf{H}}^2, \quad \forall \mathbf{p} \in \mathbf{H}^1.$$

Now using Lemma 3.1 once again we obtain

$$\lambda_2 \int_{\mathcal{O}} ||\mathbf{p}(t, a, .)||_{\mathbf{H}}^2 dtda \leq \frac{1}{2}\sum_{i=1}^N \int_0^T \int_0^L [\beta_i(t, l, \hat{P}_i^1(t)) - \beta_i(t, l, \hat{P}_i^2(t))]^2 dtdl$$

and Lemma 4.2 gives

$$\lambda_2||\mathbf{p}||_{L^2(\mathcal{O},\mathbf{H})}^2 \leq \frac{1}{2}C_3||\hat{\mathbf{p}}^1 - \hat{\mathbf{p}}^2||_{L^2(\mathcal{O},\mathbf{H})}.$$

We can choose $\lambda_2 = C_3$ and since $\mathbf{p} = \mathcal{F}\hat{\mathbf{p}}^1 - \mathcal{F}\hat{\mathbf{p}}^2$ this proves that $\mathcal{F}$ is a strict contraction on $L^2(\mathcal{O}, \mathbf{H})$. Thus it follows from Banach fixed point theorem that $\mathcal{F}$ admits a unique fixed point $\mathbf{p}$ which is the desired solution. $\square$

5 Positivity and comparison result

In this section we first show in Lemma 5.1 that the fish density population solution to our model is positive. Then a comparaison result is given in Lemma 5.2.

Lemma 5.1 *The solution* $\mathbf{p}$ *to* **problem (P)** *is nonnegative a.e. in* Q.

Proof: As in the proof of Lemma 4.3, let $\hat{\mathbf{p}}$ be given in V and let $\mathcal{F}\hat{\mathbf{p}} = \mathbf{p}$ denote the solution to (16)-(18) and satisfying $(p_i(t, 0, l)) = (\beta_i(t, l, \hat{P}_i(t)))$. Let us also assume that $\hat{\mathbf{p}} \geq 0$.
The negative parts of $p_i(0, a, l)$ and $p_i(t, 0, l)$ satisfy $(p_i(0, a, l))^- = (p_i^0(a, l))^- = 0$ and $(p_i(t, 0, l))^- = (\beta_i(t, l, \hat{P}_i(t)))^- = 0$.
One can then show using Lemma 3.1 (see [7]) that $\displaystyle\int_{\mathcal{O}} < D\mathbf{p}, \mathbf{p}^- > dtda \leq 0$.
The bilinear form e can be decomposed as $e(\mathbf{p}, \mathbf{p}^-) = e(\mathbf{p}^+, \mathbf{p}^-) - e(\mathbf{p}^-, \mathbf{p}^-)$, with
$e(\mathbf{p}^+, \mathbf{p}^-) = \displaystyle\sum_{i=1}^N b_i(p_i^+, p_i^-) + c_i(\mathbf{p}^+, p_i^-)$.
It holds that $b_i(p_i^+, p_i^-) = 0$ since one can check that $b_i(p_i, p_i^-) = -b_i(p_i^-, p_i^-)$.

Moreover, $c_i(\mathbf{p}^+, p_i^-) = -\int_0^L \sum_{j=1}^N M_{ij} p_j^+ p_i^- dl \leq 0$, since $M_{ij} p_j^+ p_i^- \geq 0$ for $i \neq j$ and $M_{ii} p_i^+ p_i^- = 0$.
We conclude that $e(\mathbf{p}^+, \mathbf{p}^-) \leq 0$.
Taking $\mathbf{q} = \mathbf{p}^-$ in Eq. 17 yields,

$$\int_{\mathcal{O}} < D\mathbf{p}, \mathbf{p}^- > dtda + \int_{\mathcal{O}} e(\mathbf{p}^+, \mathbf{p}^-) dtda - \int_{\mathcal{O}} e(\mathbf{p}^-, \mathbf{p}^-) dtda = 0$$

so that we obtain $\int_{\mathcal{O}} e(\mathbf{p}^-, \mathbf{p}^-) dtda \leq 0$. The coercivity of e gives,
$C_2 ||\mathbf{p}^-||_V \leq 0$, that is to say $\mathbf{p}$ is nonnegative.
If we define a sequence with $\mathbf{p}^1 = \hat{\mathbf{p}}$ and $\mathbf{p}^{n+1} = \mathcal{F}\mathbf{p}^n$, then from the previous lines we deduce that $\mathbf{p}^n$ is nonnegative for all $n \geq 1$. By Banach fixed point theorem this sequence converges to the solution $\mathbf{p}$ which is therefore nonnegative. $\square$

Lemma 5.2 *Let $\mathbf{p}^1$ (resp. $\mathbf{p}^2$) denote the solution to* **problem (P)** *associated with the vector of mortality rates $\mathbf{z}^1$ (resp. $\mathbf{z}^2$). If $\mathbf{z}^1 \leq \mathbf{z}^2$ then $\mathbf{p}^1 \geq \mathbf{p}^2$.*

Proof:

Step 1: Let $\hat{\mathbf{p}}^1$ and $\hat{\mathbf{p}}^2$ be given in V and satisfying $0 \leq \hat{\mathbf{p}}^1 \leq \hat{\mathbf{p}}^2$. Let $\mathbf{p}^1 = \mathcal{F}\hat{\mathbf{p}}^1$ and $\mathbf{p}^2 = \mathcal{F}\hat{\mathbf{p}}^2$ be the associated solutions defined as in the proof of Lemma 5.1. Let us show that $\mathbf{p}^1 \leq \mathbf{p}^2$.
It is clear that $\hat{P}_i^1(t) \leq \hat{P}_i^2(t)$ a.e in $(0, T)$, then since $u_i(t, P)$ is an increasing function of P it holds that $\beta_i(t, l, \hat{P}_i^1(t)) \leq \beta_i(t, l, \hat{P}_i^2(t))$ a.e in $(0, T) \times (0, L)$. The difference $\mathbf{p} = \mathbf{p}^2 - \mathbf{p}^1$ satisfies (16),(17) and

$$\begin{aligned}
&\mathbf{p}(0, l, a) = 0, \\
&\mathbf{p}(t, 0, a) = (\beta_i(t, l, \hat{P}_i^2(t))) - (\beta_i(t, l, \hat{P}_i^1(t))) \geq 0.
\end{aligned}$$

This is the same situation as in the first part of proof of Lemma 5.1 and we conclude that $\mathbf{p}$ is nonnegative that is to say $\mathbf{p}^1 \leq \mathbf{p}^2$.

Step 2: Let $\hat{\mathbf{p}} \geq 0$ be given in V. To the vectors of mortality rates $\mathbf{z}^1$ and $\mathbf{z}^2$ ($0 \leq \mathbf{z}^1 \leq \mathbf{z}^2$) we associate the bilinear forms e^1 and e^2 (see (10)-(12), note that $c_i^1(.,.) = c_i^2(.,.)$) as well as the nonlinear operators $\mathcal{F}^1$ and $\mathcal{F}^2$ defined as in the proof of lemma 5.1. They define the solutions $\mathbf{p}^1 = \mathcal{F}^1\hat{\mathbf{p}}$ and $\mathbf{p}^2 = \mathcal{F}^2\hat{\mathbf{p}}$. Let us show that $\mathbf{p}^1 \geq \mathbf{p}^2$.
$(\mathbf{p}^2 - \mathbf{p}^1)$ satisfies

$$\int_O < D(\mathbf{p}^2 - \mathbf{p}^1), \mathbf{q} > dtda + \int_{\mathcal{O}} [e^2(\mathbf{p}^2, \mathbf{q}) - e^1(\mathbf{p}^1, \mathbf{q})] dtda = 0 \qquad (21)$$

$$(\mathbf{p}^2 - \mathbf{p}^1)(0, a, l) = 0 \qquad (22)$$

$$(\mathbf{p}^2 - \mathbf{p}^1)(t, 0, l) = 0 \tag{23}$$

Let us choose $\mathbf{q} = (\mathbf{p}^2 - \mathbf{p}^1)^+$. From the equality $z_i^2 p_i^2 - z_i^1 p_i^1 = z_i^1(p_i^2 - p_i^1) + p_i^2(z_i^2 - z_i^1)$ follows that

$$\begin{aligned}
&e_i^2(\mathbf{p}^2, (p_i^2 - p_i^1)^+) - e_i^1(\mathbf{p}^1, (p_i^2 - p_i^1)^+) \\
&= c_i((\mathbf{p}^2 - \mathbf{p}^1)^+, (p_i^2 - p_i^1)^+) - c_i((\mathbf{p}^2 - \mathbf{p}^1)^-, (p_i^2 - p_i^1)^+) \\
&+ b_i((p_i^2 - p_i^1)^+, (p_i^2 - p_i^1)^+) - b_i((p_i^2 - p_i^1)^-, (p_i^2 - p_i^1)^+) \\
&+ \textstyle\int_0^L p_i^2(f_i^2 - f_i^1)(p_i^2 - p_i^1)^+ dl
\end{aligned} \tag{24}$$

We have already shown in the proof of Lemma 5.1 that $c_i((\mathbf{p}^2 - \mathbf{p}^1)^-, (p_i^2 - p_i^1)^+) \leq 0$ and that $b_i((p_i^2 - p_i^1)^-, (p_i^2 - p_i^1)^+) = 0$. Moreover since $\mathbf{p}^2$ is nonnegative the last term of equality (24) is nonnegative. Then we obtain that

$$e^2(\mathbf{p}^2, (\mathbf{p}^2 - \mathbf{p}^1)^+) - e^1(\mathbf{p}^1, (\mathbf{p}^2 - \mathbf{p}^1)^+) \geq e^1((\mathbf{p}^2 - \mathbf{p}^1)^+, (\mathbf{p}^2 - \mathbf{p}^1)^+).$$

Since $(\mathbf{p}^2 - \mathbf{p}^1)$ satisfies (22) and (23) it also holds that

$$\int_O < D(\mathbf{p}^2 - \mathbf{p}^1), (\mathbf{p}^2 - \mathbf{p}^1)^+ > dtda \geq 0,$$

so that

$$\int_{\mathcal{O}} e^1((\mathbf{p}^2 - \mathbf{p}^1)^+, (\mathbf{p}^2 - \mathbf{p}^1)^+) dtda \leq 0,$$

and using the coercivity of e^1 we finally obtain $\mathbf{p}^2 \leq \mathbf{p}^1$.

Step 3: Let $\hat{\mathbf{p}} \geq 0$ be given in V. We define two sequences $(\mathbf{p}^{1,n})_{n\geq 1}$ and $(\mathbf{p}^{2,n})_{n\geq 1}$ by $(\mathbf{p}^{1,1} = \hat{\mathbf{p}},\ \mathbf{p}^{1,n+1} = \mathcal{F}^1\mathbf{p}^{1,n})$ and $(\mathbf{p}^{2,1} = \hat{\mathbf{p}},\ \mathbf{p}^{2,n+1} = \mathcal{F}^2\mathbf{p}^{2,n})$. From **step 2** follows that $\mathbf{p}^{1,2} \geq \mathbf{p}^{2,2}$.
In addition to $\mathbf{p}^{1,3} = \mathcal{F}^1\mathbf{p}^{1,2}$ and $\mathbf{p}^{2,3} = \mathcal{F}^2\mathbf{p}^{2,2}$, let us define $\mathbf{q}^3 = \mathcal{F}^2\mathbf{p}^{1,2}$. The inequality $\mathbf{p}^{1,3} \geq \mathbf{q}^3$ follows from **step 2**, whereas $\mathbf{p}^{2,3} \leq \mathbf{q}^3$ follows from **step 1**. Therefore $\mathbf{p}^{1,3} \geq \mathbf{p}^{2,3}$. An induction then shows that $\mathbf{p}^{1,n} \geq \mathbf{p}^{2,n}$, $\forall n \geq 1$ and since the sequences converge to the solution $\mathbf{p}^1$ and $\mathbf{p}^2$ of **problem (P)** associated with the vector of mortality rates $\mathbf{z}^1$ and $\mathbf{z}^2$ respectively, the proof is complete. □

6 Concluding remarks

In this paper we have investigated a multi-region nonlinear age-size structured fish population model. The model was formulated in a generic way so that it can be potentially used for various fish species. We formulated an initial boundary-value problem and proved existence and uniqueness of a positive

weak solution. We also proved a comparison result which shows that the variations in the mortality rate in each region have consequences on the population of fish in every regions.
Other important problems need to be addressed now and are currently under progress. The first one concerns the numerical implementation of this model. In order to integrate numerically system (1)-(4) we use the characteristic method. Indeed this system can be viewed as a collection of systems of parabolic equations on the characteristic lines

$$S = \{(t_0 + s, a_0 + s);\ s \in (0, s_{max}(t_0, a_0))\},$$

where $(t_0, a_0) \in \{0\} \times (0, A) \cup (0, T) \times \{0\}$. Each of these systems is then integrated in time with an operator splitting method using the Lie formula ([15], [16]).
The second problem concerns the estimation of the different badly known parameters of the model (growth, mortality and migration rates) from the data available for fisheries and mentioned in the Introduction. In order to solve numerically this inverse problem, the implementation of a variational data assimilation method is under progress. The objective is to obtain a synthetic representation of the real system combining theoritical knowledge (the model) and experimental knowledge (the data).

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